HYBRIDIZATION BETWEEN THE WESTERN ATLANTIC ANGELFISHES, *HOLACANTHUS ISABELITA* AND *H. CILIARIS*[1]

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ABSTRACT

The angelfishes *Holacanthus isabelita* and *H. ciliaris* were studied to determine the status of angelfishes that possessed coloration intermediate between these species. Due to the lack of consistent meristic differences, analysis was primarily accomplished by using portions of the general color pattern of adults, but gonads, behavior, and relative populations were also investigated. It was found that these intermediate individuals were hybrids between the two above species. The type specimens of *Holacanthus ciliaris* var. *Bermudensis* Goode, 1876, and *Holacanthus townsendi* (Nichols & Mowbray, 1914) were also intermediate and were judged to be hybrids.

INTRODUCTION

The angelfishes of the family Chaetodontidae make up a group of brightly colored, laterally compressed fishes characterized by a single, large, posteriorly pointing spine on the angle of the preoperculum. The group, circumtropical in extent, primarily occupies coral reefs and rocky areas in shallow marine waters, but some species range deeper than 200 feet.

Six species occur in the Western Atlantic: *Centropyge argi* (pigmy angelfish), *Holacanthus tricolor* (rock beauty), *Pomacanthus arcuatus* (gray angelfish), *Pomacanthus paru* (French angelfish), *Holacanthus isabelita* (blue angelfish), and *Holacanthus ciliaris* (queen angelfish). All are found in southeast Florida. The name black angelfish is commonly applied to the juveniles of the gray and of the French angelfishes in Florida, and to the rock beauty in Bermuda.

The taxonomic positions of four of these species, up to now, have been somewhat uncertain. The main reason is that the gray and French angelfishes and the blue and queen angelfishes form two pairs of very similarly colored juveniles, whereas adults of each species are completely different from the juveniles and from each other. The only useful meristic character separating most specimens of the gray and French angelfishes is the usual presence of nine dorsal-fin spines in the gray angelfish, and

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usually ten spines in the French angelfish. On the other hand, both the blue and queen angelfishes usually possess 14 dorsal-fin spines, but the blue angelfish usually has 19 dorsal- and anal-fin rays, whereas the queen angelfish usually has 20. Unfortunately, these counts are only partially useful in identifying specimens, leaving coloration as the only reliable guide to these species. Since the patterns are distinct, coloration would seem to offer reliable identification. This is true for the gray and French angelfishes, but adults with coloration intermediate between the blue and queen angelfishes are often found.

Nichols & Mowbray (1914) described one of these intermediates as a new species of angelfish, *Holacanthus townsendi*. However, the name was not generally accepted, and authors continued to identify these individuals as blue or queen angelfishes. Longley, however (*in* Longley & Hildebrand, 1941: 154), concluded that this form was a cross between the two species, but gave no supporting evidence to prove the contention.

The present paper is an attempt to clarify the relationships among the blue and queen angelfishes, and the intermediates.

Acknowledgments

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Materials and Methods

Almost all of the fishes used in this study were collected by the author from southeast Florida and the Florida Keys. Others were from deep water off northeast Florida and the Carolinas (caught by M/V Silver Bay). Two were from the Bahamas (Seaquarium).

Due to the very close meristic and morphological features of the blue and queen angelfishes (Tables 1 and 2), it was necessary to base the analysis of taxonomic relationships primarily on the coloration of the adults. Eight separate and conspicuous patterns, and one variable but useful morphological character, were used. The locations of these features are: nape, area around bases of anterior dorsal spines, iris, posterior edge of operculum, base and rays of pectoral fin, large body scales, last rays of anal fin below the caudal peduncle, caudal fin, and preopercular spines.

The system of analysis was adapted from that used by Sibley (1950: 112) for studying a species complex of birds in Mexico. The patterns described in Table 3 and illustrated in Figures 1 to 9 were rated from 0, indicating the most extreme form of the pattern displayed on the blue angelfish, to 4, indicating the most extreme form of the corresponding pattern displayed on the queen angelfish. Intermediate conditions were designated by 1, 2, and 3, or by 2 if only one intermediate condition could be reliably identified. All drawings are from specimens of from 200 to 250 mm SL.

Figure 10 shows the variation in the relative sizes of the small accessory preopercular spines as compared to the main spine at the angle. The length of the largest accessory spine was divided by the length of the main spine (measured as indicated in Figure 9) and plotted against the standard length of the fish.

Tables 4 to 6 show the combinations of pattern variations displayed by the individuals examined in this study, together with the numbers of individuals displaying these combinations.

Testes and ovaries of the two species, and of the intermediates, were examined macroscopically, then preserved in Bouin's solution, sectioned, stained, and examined microscopically.

In addition, scuba observations were made on the social behavior of the fishes, and population surveys were made, in five main types of habitats occupied by these forms. The surveys were made by swimming at a constant speed in a straight line for measured lengths of time, observing the swath of substrate visible, and counting all angelfish seen during this time. The width of the survey zone varied from 10 to 40 feet (estimated visually), depending on the clarity of the water. Times of survey varied from 4 to 50 minutes, depending on the extent of suitable habitat. Due to the very variable occurrence of angelfishes, a survey was started only when the first individual was encountered.

Meristic Variation and General Coloration

Selected meristic data taken from blue and queen angelfishes and the intermediates, in an attempt to differentiate among them, are shown in Table 1. For the dorsal and anal fins, all specimens available were used,

TABLE 1

SELECTED MERISTIC DATA FROM SPECIMENS OF *Holacanthus isabelita*, *H. ciliaris*, AND INTERMEDIATES[1]

	H. isabelita (blue angelfish)	intermediate	*H. ciliaris* (queen angelfish)
Dorsal fin	XIII,18 to XV,21 (XIV,19)	XIV,17 to XV,20 (XIV,19)	XIII,19 to XV,21 (XIV,20)
Anal fin	III,18 to IV,20 (III,19)	III,18 to IV,20 (III,19)	III,19 to III,20 (III,20)
Pectoral fin	18 to 20 (19)	18 to 20 (19)	18 to 20 (19)
Lateral-line scales	41 to 48 (45)	40 to 47 (45)	40 to 46 (44)
Gill rakers	19 to 22 (19)	17 to 22 (20, 21)	18 to 21 (19)

[1] Numbers in parentheses are modes.

but for counts of the pectoral fin, lateral-line scales, and gill rakers, 25 specimens each were examined.

Due to the identity or essential similarity of these counts, none of them could be used to differentiate the species completely. The dorsal- and anal-fin rays, however, do show variations in number within a species. Table 2 shows the percentages of the specimens examined that possess certain numbers of spines and rays. It can be seen that most blue angelfishes possess 19 dorsal- and anal-fin rays, whereas most queen angelfishes possess 20. Of the intermediates examined, most possess 19 dorsal- and anal-fin rays, but the percentages are intermediate between those of the two species.

The numbers of the various head spines were counted in hopes of revealing a difference, but no consistent differences were found. The number of preopercular spines, for instance, varied considerably and depended greatly on the size of the individual. Also, there was considerable overlap in number between the species, and uncertainty whether a particular serration should be counted as a spine or not. The number of accessory scales covering the large scales of the body similarly did not yield distinguishing values.

In addition to the meristic data, proportional measurements of head length, snout length, orbit length, body depth, dorsal fin length, anal fin length, and pectoral fin length show (throughout the size range of fishes collected) essentially synonymous ranges of values, according to size of fish.

There seems to be slight morphological differentiation with increase in size (of the large adults), such as the bulging nape of large blue angelfish, but this could not be used to differentiate the smaller individuals.

The coloration of the small juveniles of both species is extremely similar. Both have a dark blue background color, segmented by five

TABLE 2

PERCENTAGES OF SPECIMENS OF *Holacanthus isabelita, H. ciliaris,* AND INTERMEDIATES EXAMINED, SHOWING PARTICULAR NUMBERS OF DORSAL- AND ANAL-FIN SPINES AND SOFT RAYS

Identification	Number of specimens	Spines					Rays				
		3	4	13	14	15	17	18	19	20	21
				DORSAL FIN							
H. isabelita (Blue angelfish)	187	—	—	3	95	2	—	17	68	14	1
intermediate	40	—	—	—	95	5	2.5	2.5	55	40	—
H. ciliaris (queen angelfish)	87	—	—	5	93	2	—	—	38	57	5
				ANAL FIN							
H. isabelita (blue angelfish)	187	99.5	0.5	—	—	—	—	16	76	7	—
intermediate	40	97.5	2.5	—	—	—	—	8	58	35	—
H. ciliaris (queen angelfish)	87	100.0	—	—	—	—	—	—	31	69	—

major vertical bluish-white bars located: anterior to the eye, posterior to the eye, on the anterior part of the body, on the posterior part of the body, and just anterior to the caudal peduncle. There may be additional fainter and narrower bars on the body, especially in the blue angelfish, but these other bars usually do not extend completely across the body. Two pale areas, located anterior to the first bar and on the ventral half of the body between the second and third bars, are yellow to pale orange on the live blue angelfish, and orange on the live queen angelfish.

At this size and color pattern, the only reliable way to determine the species is by the curvature of the fourth bar from the head, a character that remains reliable until the bars disappear. In the blue angelfish this bar is straight (on the body) while that of the queen angelfish is distinctly curved. Juveniles possessing a bar that is only slightly curved may be of the intermediate hybrid form.

The color patterns described above change slowly with growth, especially that of the blue angelfish, which acquires large amounts of yellow on the dorsal and anal fins. However, when the adult coloration begins to develop, changes in both coloration and pattern are rapid, involving the loss of the bars, and resulting in stable patterns vastly different from those of the juveniles and unique for the species.

The coloration of blue angelfishes (Fig. 12) larger than about 120 mm SL is composed of a fairly uniform bluish-whitish-brownish tone over the head and body, and on the dorsal, anal, and caudal fins. The thoracic and

TABLE 3

DESCRIPTION OF PATTERNS USED IN ANALYSIS OF HYBRIDIZATION BETWEEN *Holacanthus isabelita* AND *Holacanthus ciliaris*

Pattern No.	Pattern and location	*Holacanthus isabelita* Rating	*Holacanthus isabelita* Description	Intermediate Rating	Intermediate Description	*Holacanthus ciliaris* Rating	*Holacanthus ciliaris* Description
1	Ocellus (on nape)	0	Indefinite blue streak extending from eyes and fading into base of dorsal fin.	1 2 3	Definite, uniformly blue disc. Blue disc with a few central black spots. Wide blue ring around a small, central, black disc.	4	Narrow blue ring around a large black disc speckled with blue.
2	Orange streak (around bases of anterior dorsal spines)	0	No different in color from the surrounding parts of the body.	2	Small streak of orange, widest in the anterior part, tapering posteriorly into the proximal portion of the dorsal fin.	4	Large streak of orange, as wide as ocellus in anterior portion, tapering posteriorly into the proximal portion of the dorsal fin.
3	Blue spots (iris of eye)	0	No trace of blue on periphery.	1 2 3	Small blue spot on dorsal periphery. Larger blue streak on dorsal periphery and small blue spot on ventral periphery. Large blue streaks on both dorsal and ventral periphery.	4	Blue band extending entirely around the periphery, except in the anterior quadrant.
4	Blue stripe (posterior edge of operculum)	0	Dorsal half of blue stripe similar in width to ventral half.	2	Dorsal half of stripe wider than ventral half, but with an irregular anterior border.	4	Dorsal half of stripe much wider than ventral half, widest dorsally, with definite regular anterior margin.

TABLE 3 (CONTINUED)

Pattern No.	Pattern and location	*Holacanthus isabelita* Rating	*Holacanthus isabelita* Description	Intermediate Rating	Intermediate Description	*Holacanthus ciliaris* Rating	*Holacanthus ciliaris* Description
5	Blue and black pattern (base and rays of pectoral fin)	0	Uniform blue area merging into similar color over thorax region and extending into proximal ⅔ of fin rays. Yellow, then transparent, borders on distal ⅓ of rays.	1	Distinct, somewhat circular blue area at base of fin, extending slightly onto rays. Rest of fin yellow.	4	Very large black area displacing almost all of the blue area, except for a narrow band of blue along the dorsal and anterior edge of the black area. Rest of fin yellow.
				2	The distinct blue area extends farther on fin and possesses a number of small elongated black markings on the bases of the upper pectoral rays. Rest of fin yellow.		
				3	Large, thick, blunt, solid-black crescent on bases of upper pectoral rays, entirely surrounded by the blue area. Rest of fin yellow.		
6	Coloration (edge of large scales of body)	0	Narrow whitish stripe on exposed posterior edge.	2	Yellow crescent on exposed posterior edge.	4	Orange triangle on posterior half of exposed portion of scale.
7	Blue and black pattern (last rays of anal fin, below the caudal peduncle)	0	Wide, indefinite, yellow border.	1	Very narrow and short blue border, with wide submarginal yellow band.	4	Very wide blue border, very narrow submarginal yellow band, and large black smudge covering rays of fin, out to the blue border.
				2	Blue border and yellow submarginal band of about equal widths.		
				3	Wide blue border, very narrow submarginal yellow band.		

TABLE 3 (CONTINUED)

Pattern No.	Pattern and location	*Holacanthus isabelita* Rating	*Holacanthus isabelita* Description	Intermediate Rating	Intermediate Description	*Holacanthus ciliaris* Rating	*Holacanthus ciliaris* Description
8	Coloration (caudal fin)	0	Narrow, yellow, posterior border; rest of fin dark.	1	Wide, yellow, posterior edge, with yellow dorsal and ventral extensions towards base of fin. Rest of fin dark.	4	Entire caudal fin bright yellow-orange, with sharp, straight, vertical, anterior border.
				2	Yellow covers about distal ½ of fin, shading anteriorly into dark part of fin. Many salmon-colored specks along the indefinite anterior border of the yellow color.		
				3	Most of fin yellow, with small dark area at anterior center of fin.		
9	Sizes (preopercular spines)	0	Largest of the small spines ½ or more the length of the primary spine at the angle of the preopercle.	2	Largest of the small spines ¼ to ½ the length of the primary spine.	4	Largest of the small spines ¼, or less, the length of the primary spine.

nape region, the distal horizontal edges of the dorsal and anal fins, the preopercular spines, and the proximal half of the pectoral fin are bright blue. The distal edge of the caudal fin, the vertical distal edges of the dorsal and anal fins, the submarginal edge of the pectoral fin, and the ventral fin are yellow. There may be very narrow borders of blue on the vertical portions of the dorsal and anal fins, and blue spots on the iris of the eye. The large scales on the body are edged with white.

The coloration of queen angelfishes (Fig. 15) larger than about 100 mm SL consists mainly of yellow on the head, and deep blue on the body, shading to greenish dorsoposteriorly. The black and bright blue markings are displayed on the nape, base of pectoral fin, and the last few rays of the dorsal and anal fins. Bright blue is present on the iris of the eye, the preopercular spines, the edge of the opercle, and the borders of the dorsal and anal fins. The caudal, ventral, and pectoral fins are entirely yellow. Orange triangles are present on the large scales of the body, and an orange streak starts posterior to the ocellus (on the nape) and extends into the dorsal fin. Brownish orange is present on the trailing filaments of the dorsal and anal fins.

The overall coloration of the adult intermediates found in the habitats is pale blue and yellow on the head and body, becoming darker and faintly greenish dorsoposteriorly on the body and dorsal and anal fins (Figs. 13 and 14).

The blue, yellow, and black markings on the head and body are basically similar to those of the queen angelfish, but are underdeveloped or lacking. The proximal portion of the caudal fin is dark, the rest yellow. The large scales of the body possess yellow crescents.

Evaluation of Patterns Analyzed

Table 3 and Figures 1 to 9 describe and illustrate all patterns used in this study. Each variation of a pattern was drawn according to its development on the fishes, and was used if the variation could be reliably identified. The location and evaluation of each pattern is as follows.

Nape.—(Fig. 1.) The ocellus, a very striking mark present on the nape of the queen angelfish, is completely absent on the blue angelfish. In the latter, its location is covered by an indefinitely defined streak of pale blue that extends anteriorly between the eyes and posteriorly into the dorsal fin. This streak is poorly retained in preserved specimens, but the other variations are more sharply defined on the fish and are more completely retained. The ocellus of the queen angelfish, for instance, is retained as a blue or dark band encircling a black or brown area containing paler flecks.

Area Around Bases of Anterior Dorsal Spines.—(Fig. 2.) This area,

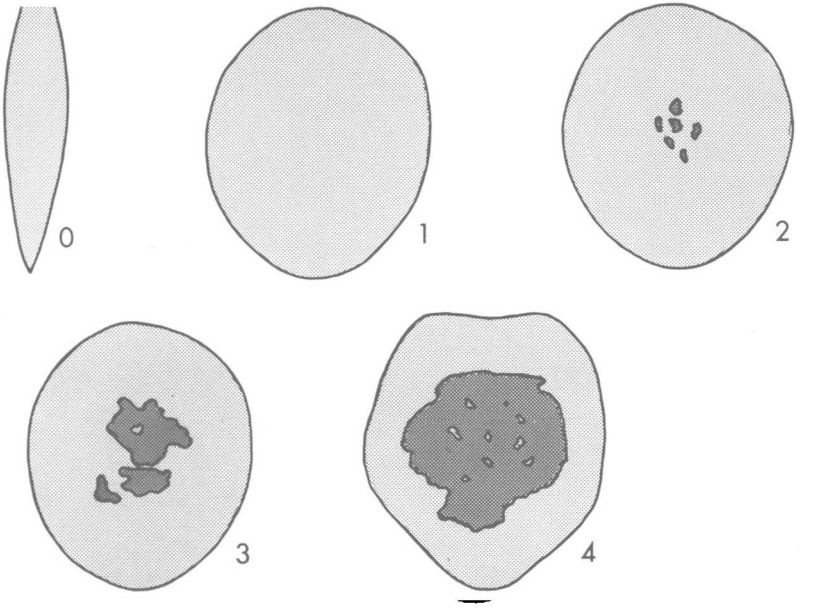

FIGURE 1. Variations of development of ocellus on the nape of: the blue angelfish (typically 0 on a rating scale of 0 to 4), the queen angelfish (typically 4), and the hybrid form (typically 1, 2, or 3). Medium hatching represents blue coloration, dark hatching represents black.

occupied in the blue angelfish by the blue streak on the nape, is decorated by an orange streak in the queen angelfish. The edges of the orange streak are not sharply defined, but blend into the bluish background. This pattern is retained in preserved specimens as a pale streak.

Iris.—(Fig. 3.) The pattern consists of sharply defined blue spots or bands on the outer edge of the yellow iris. The spot on the upper part of the iris is retained in preserved specimens as a dark area, but that on the lower part of the iris may fade completely.

Posterior Edge of Operculum.—(Fig. 4.) The pattern on the blue angelfish is confined to the opercular membrane, but the upper portion of that of the queen angelfish expands onto the operculum itself. Both patterns are sharply defined. The intermediate pattern, however, fades into the background color along its anterior edge. The pattern is usually retained on preserved specimens, but may fade on those preserved for a long time.

Base and Rays of Pectoral Fin.—(Fig. 5.) In the blue angelfish, the blue background color spreads over the base and into the proximal half of the pectoral fin. A submarginal yellow band follows, then a distal trans-

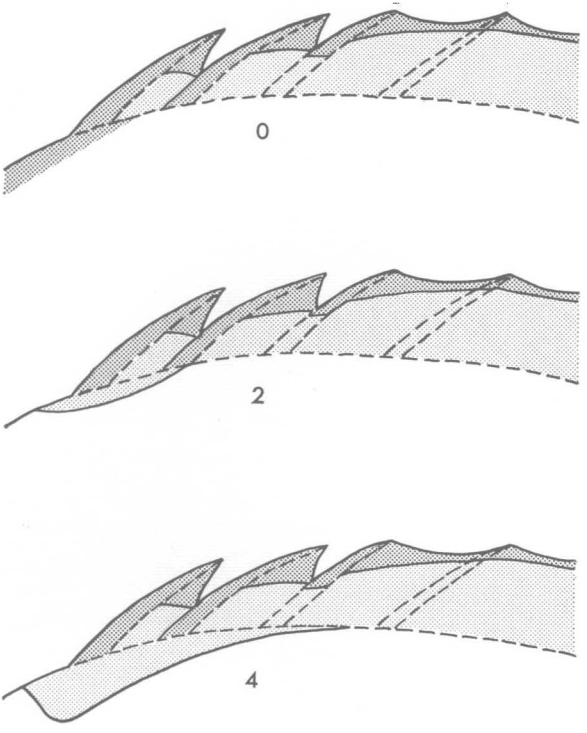

FIGURE 2. Variations of development of orange streak around bases of anterior dorsal-fin spines of: the blue angelfish (typically 0 on a rating scale of 0 to 4), the queen angelfish (typically 4), and the hybrid form (typically 2). Pale hatching represents orange coloration, medium hatching represents blue.

parent border. These colors are not sharply separated from each other. In the other variations of this pattern, however, all colors have definite borders. In preserved specimens, the black central area on the queen angelfish and intermediates may fade to pale or dark gray with a narrow, darker marginal line. This line can be mistaken for the intermediate pattern 3, where the blue bar surrounds the black area.

Exposed Portions of Large Scales of Body.—(Fig. 6.) The patterns in fresh specimens are sharply defined and distinct, especially on the central portion of the body. Toward the edges of the body, the patterns become smaller and circular. These patterns are very indistinct on preserved specimens because the color disappears and the exposed portion of the scale becomes white, producing a misleading triangular white pattern. A close examination usually reveals traces of the original pattern.

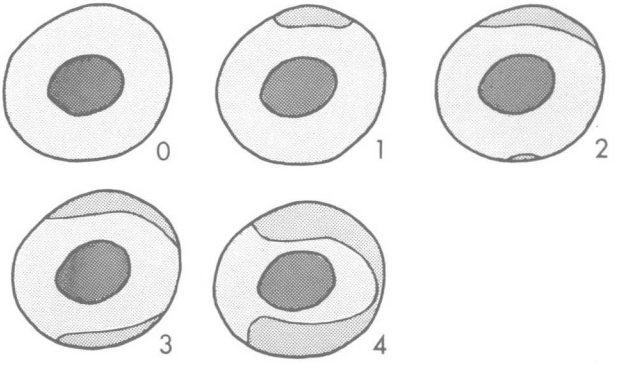

FIGURE 3. Variations of development of blue spots on iris of eye of: the blue angelfish (typically 0 or 1 on a rating scale of 0 to 4), the queen angelfish (typically 3 or 4), and the hybrid form (typically 1, 2, or 3). Palest hatching represents yellow coloration, medium hatching represents blue, and darkest hatching represents black.

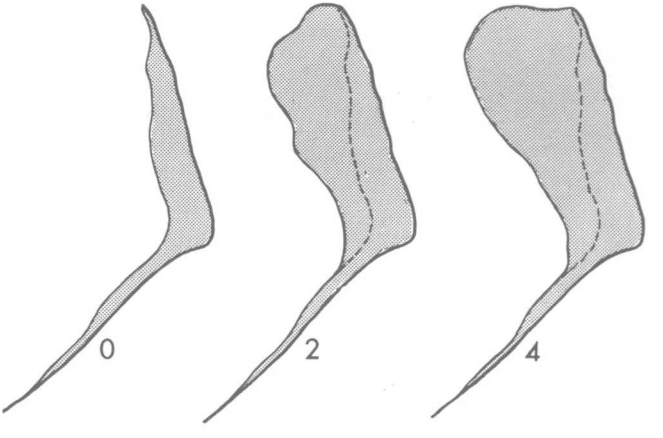

FIGURE 4. Variations of development of blue bar on posterior edge of operculum of: the blue angelfish (typically 0 on a rating scale of 0 to 4), the queen angelfish (typically 4), and the hybrid form (typically 2). The hatching represents blue coloration.

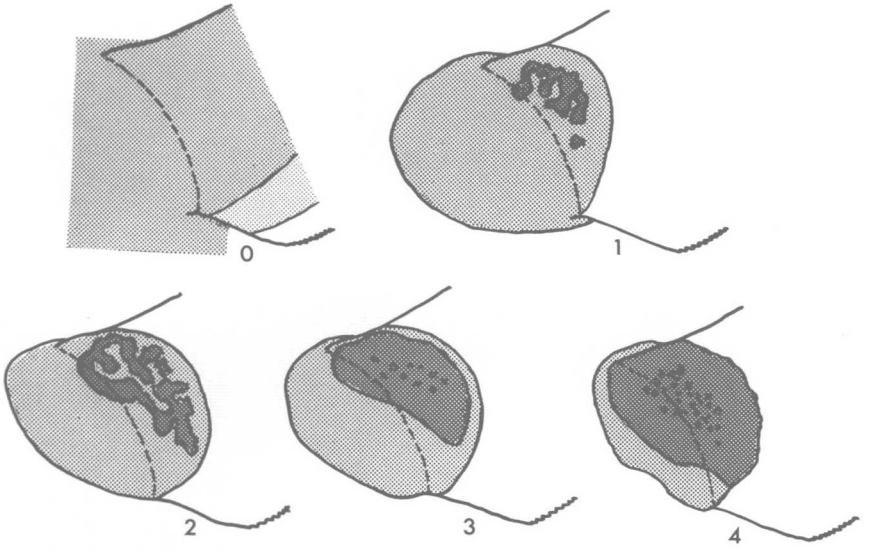

FIGURE 5. Variations of development of pattern on base and rays of pectoral fin of: the blue angelfish (typically 0 on a rating scale of 0 to 4), the queen angelfish (typically 4), and the hybrid form (typically 1, 2, or 3). Palest hatching represents yellow coloration, medium hatching represents blue, and darkest hatching represents black. The squared edge of the hatching on the "0" drawing indicates that the color extends beyond the area drawn. The dashed line indicates the bases of the fin rays. The blank portion of the fin is transparent in the "0" drawing, yellow in the other drawings.

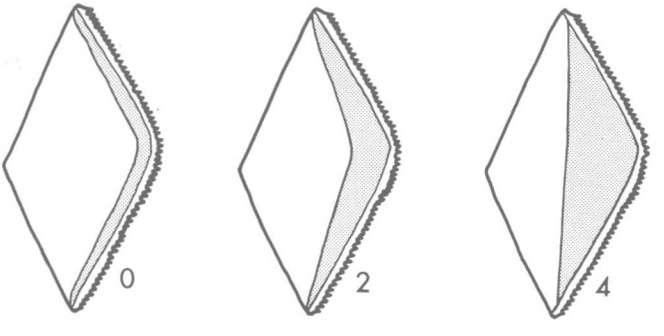

FIGURE 6. Variations of development of pattern on exposed portions of large scales of the body of: the blue angelfish (typically 0 on a rating scale of 0 to 4), the queen angelfish (typically 4), and the hybrid form (typically 2). Accessory scales, which cover the anterior halves of the exposed portions of the scales, are omitted for simplicity. From left to right, the hatching represents white, yellow, and orange coloration.

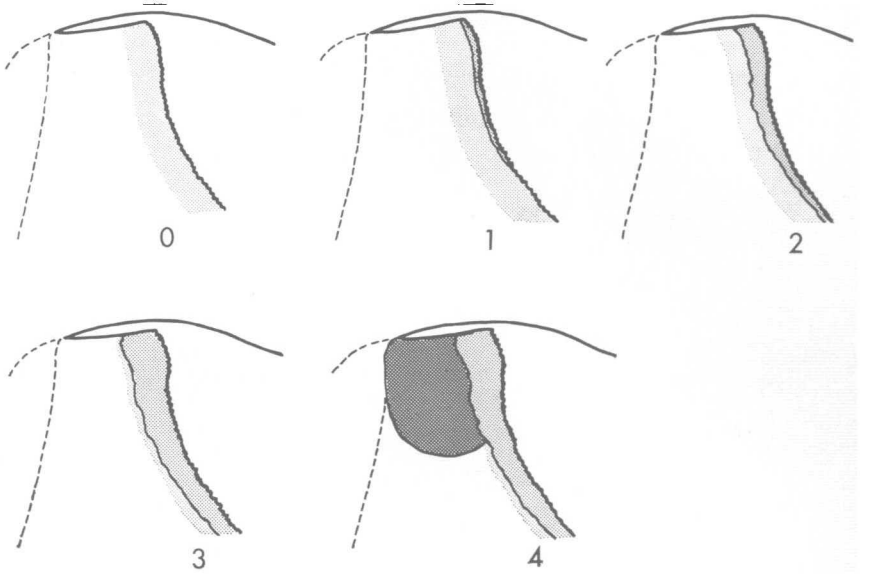

FIGURE 7. Variations of development of pattern on last few rays of anal fin, below caudal peduncle, of: the blue angelfish (typically 0 on a rating scale of 0 to 4), the queen angelfish (typically 4), and the hybrid form (typically 1, 2, or 3). Palest hatching represents yellow coloration, medium hatching represents blue, and darkest hatching represents black.

Last Rays of Anal Fin, Below the Caudal Peduncle.—(Fig. 7.) The black blotch is indistinct in outline, but is retained unchanged in preservation. The blue border is distinct, and also remains, usually as a dark area. The submarginal yellow band, however, is pale and indistinct in the living specimen, and fades rapidly upon preservation, especially in the queen angelfish. In the blue angelfish and the intermediates, it shows as a pale area.

Caudal Fin.—(Fig. 8.) The yellow portion of the fin of the queen and the blue angelfishes is separated abruptly from the body color, but in the intermediates, the yellow grades very gradually into the darker body color. A rating is made on the basis of the area on the fin where this transition occurs. Unfortunately, this transition area on the intermediates disappears almost completely after lengthy preservation.

Preopercular Spines.—(Fig. 9.) This morphological character was rated visually, partly by noticing the absolute size of the accessory spines, and by comparing the largest accessory spine to the main spine below it at the angle of the preopercle, at the same time taking the size of the fish

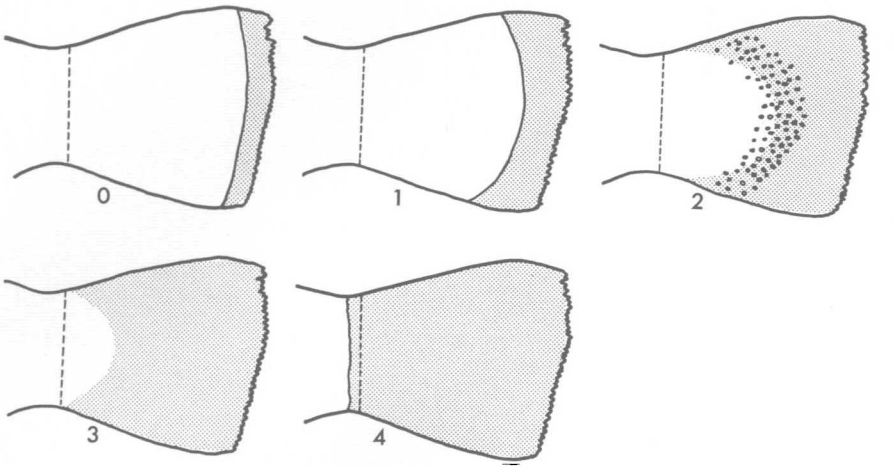

FIGURE 8. Variations of development of pattern on caudal fin of: the blue angelfish (typically 0 on a rating scale of 0 to 4), the queen angelfish (typically 4), and the hybrid form (typically 1, 2, or 3). Hatching represents yellow coloration. The blank portion of the fin is dark. Spots on the "2" drawing are salmon-colored.

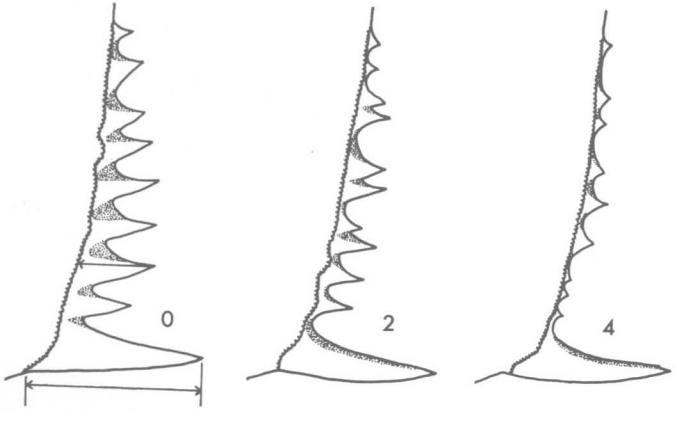

FIGURE 9. Variations in sizes of preopercular spines of 200-mm-SL specimens of: the blue angelfish (typically 0 on a rating scale of 0 to 4), the queen angelfish (typically 4), and the hybrid form (typically 2). The spines on the lower horizontal portion of the preoperculum are omitted. Dotted sections denote areas covered only by membrane. The wavy line indicates posterior edge of scale area. Arrows indicate the method of measuring lengths of spines.

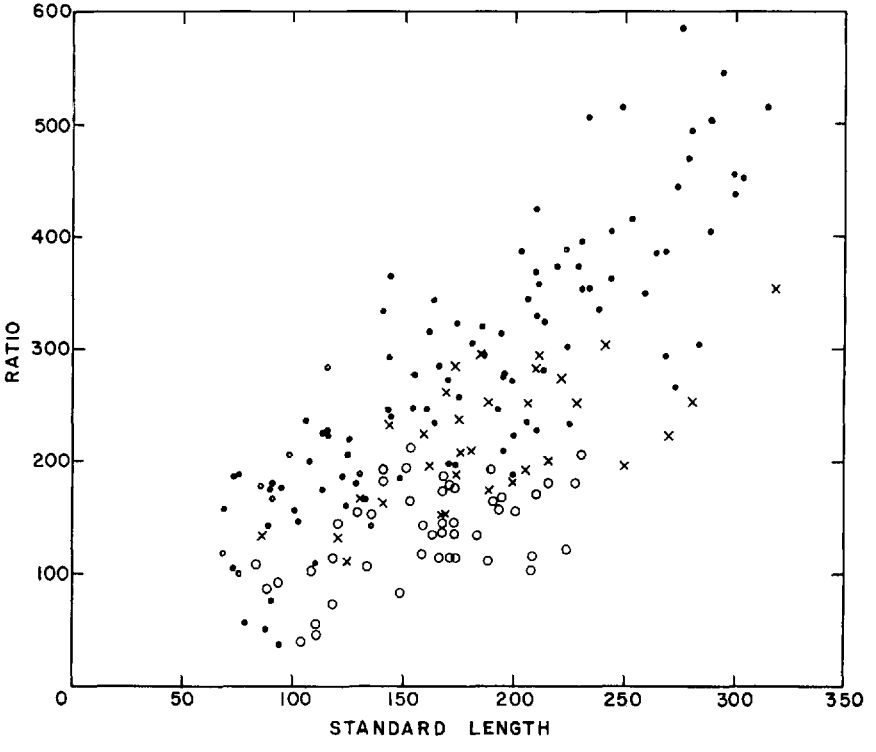

FIGURE 10. Relative lengths of largest accessory spine and main spine at the angle of the preopercle of: the blue angelfish (•), the queen angelfish (o), and the hybrid form (x). Length of accessory spine is divided by length of main spine and plotted against standard length of fish. Spines were measured as in Figure 9.

into account. Figure 9 illustrates typical spine patterns drawn from specimens of about 200 mm SL. Larger individuals, especially of the blue angelfish, show patterns with the accessory spines far larger, reaching almost to the same distance posteriorly as the main spine. Judging from the specimens seen, accessory spines of the queen angelfish grow only a little larger proportionally than those indicated in Figure 9.

Figure 10 shows that the ratios of accessory spine to main spine, although generally separate for the blue and the queen angelfishes, do merge somewhat. Intermediate angelfishes show ratios along this borderline.

All individuals less than 50 mm SL, and most of those less than 75 mm SL, possessed accessory spines that were merely serrations. Only during the change from the juvenile to the adult color patterns did these serrations start to increase in size, one by one. The development of the

serrations is essentially symmetrical on each preoperculum. The spines are sheathed with blue-pigmented skin, and are unscaled.

Remarks.—Several assumptions were made for this method of rating: that characters do not shift in rating value within the size range of specimens rated, that the characters chosen vary independently from one another, that genes of one species are not dominant over those of the other, and that characters are correctly evaluated.

Both males and females of adult blue and queen angelfishes as well as intermediates have been found, ruling out the possibility of sexual dimorphism to explain the color differences.

Analysis of Hybridization

The ratings for the blue angelfish (Table 4) show that the most conservative patterns, of those examined, are: lack of an orange streak around the base of the dorsal fin, the coloration of the pectoral fin, and the white edges of the large scales of the body. Rarely, the border of the opercle will have a wider blue bar than normal, and the caudal fin a wider yellow border. Very occasionally, a very poorly developed ocellus will be seen. Most of the fishes have one blue spot on the dorsal part of the iris of the eye, and most have a very narrow and short blue edge on the vertical portion of the anal fin (and dorsal fin as well). About 30 per cent of the individuals have smaller preopercular accessory spines than normal, and, very rarely, one with spines characteristic of the queen is seen.

The most conservative characters of the queen angelfish (Table 6) are: the ocellus, a wide blue stripe on the posterior edge of the operculum, the coloration of the base of the pectoral fin, the pattern on the anal fin, and an entirely yellow-orange caudal fin. Very rarely, an individual may be seen with an underdeveloped pectoral-fin pattern. Rare, also, is a larger-than-normal set of accessory spines. Slightly more often, yellow crescents on the scales are encountered. The greatest deviation from normal is shown in the width of the orange streak on the nape area, and in the extent of blue on the iris of the eye.

The characters of intermediates (Table 5) show extreme variations from individual to individual. Most have a median development, but often a pattern characteristic of the blue or the queen angelfishes appears. The most median characters seem to be: a narrow orange streak on the nape, crescents on the body scales, and medium-sized accessory spines.

The rating for each pattern was totaled for each fish, and the totals graphed in Figure 11 as a frequency distribution. A total rating of 0 would indicate a blue angelfish extreme in all characters used, while 36 would indicate a queen angelfish extreme in all characters used. Actually, 0 to 8 may be considered ratings of the blue angelfish, accounted for by

TABLE 4

PATTERN COMPOSITION ON INDIVIDUALS OF *Holacanthus isabelita*[1]

Total rating	Pattern number									Number of individuals
	1	2	3	4	5	6	7	8	9	
0	0	0	0	0	0	0	0	0	0	1
1	0	0	1	0	0	0	0	0	0	9
	0	0	0	0	0	0	1	0	0	5
2	0	0	1	0	0	0	1	0	0	12
	1	0	1	0	0	0	0	0	0	4
	0	0	2	0	0	0	0	0	0	3
	1	0	0	0	0	0	1	0	0	1
	0	0	1	0	0	0	0	1	0	1
	0	0	0	2	0	0	0	0	0	1
	0	0	0	0	0	0	0	0	2	1
3	0	0	1	0	0	0	0	0	2	5
	1	0	1	0	0	0	1	0	0	2
	0	0	0	0	0	0	1	0	2	2
	0	0	2	0	0	0	0	1	0	1
4	0	0	1	0	0	0	1	0	2	4
	1	0	0	0	0	0	1	0	2	1
	1	0	1	0	0	0	2	0	0	1
	2	0	2	0	0	0	0	0	0	1
	0	0	2	0	0	0	0	0	2	1
5	0	0	4	0	0	0	1	0	0	1
	0	0	1	0	0	0	1	1	2	1
	1	0	1	0	0	0	1	0	2	1
6	0	0	1	0	0	0	0	1	4	1
	0	0	2	2	0	0	0	0	2	1
	2	0	2	2	0	0	0	0	0	1
7	2	0	1	0	0	0	2	0	2	1
	1	0	2	2	0	0	0	0	2	1
	1	2	1	0	1	0	1	1	0	1
8	2	0	0	0	2	0	2	0	2	1

[1] For explanation of numerical ratings, see text.

infraspecific variation, and, similarly, 30 to 36 may be considered characteristic of the queen angelfish. Median rating values would indicate intermediates.

Typical queen angelfishes thus seem to be less variable than blue angelfishes, both in the total amount of variation, and in the pattern composition of individuals. Rarely are all patterns displayed by an individual blue angelfish rated as 0, while a large number of queen angelfish have all patterns rated as 4. On the other hand, intermediate individuals showed

TABLE 5

PATTERN COMPOSITION ON INDIVIDUALS OF THE HYBRID, *Holacanthus isabelita* × *Holacanthus ciliaris*[1]

Total rating	Pattern number									Number of individuals
	1	2	3	4	5	6	7	8	9	
15	2	0	3	2	2	0	2	2	2	1
	1	0	4	2	1	2	2	1	2	1
16	1	2	2	0	3	2	2	2	2	1
17	2	0	4	2	1	2	3	1	2	1
	2	2	3	0	3	2	3	2	0	1
	2	2	1	2	3	0	3	2	2	1
	2	2	1	2	2	2	2	2	2	1
18	2	2	1	2	3	2	3	3	0	1
	1	2	3	2	3	2	2	1	2	1
	1	0	3	4	2	2	2	2	2	1
	1	0	3	2	3	2	3	2	2	1
	3	0	1	2	4	2	2	2	2	1
19	1	2	4	2	2	2	2	2	2	1
	1	2	2	2	2	2	3	3	2	1
	1	2	3	2	3	2	2	2	2	1
	2	2	2	2	3	2	2	2	2	1
20	1	2	4	2	3	2	3	1	2	1
	1	2	3	2	3	2	2	3	2	1
	2	2	2	2	3	2	2	3	2	1
	2	2	3	2	3	2	2	2	2	1
21	1	2	2	4	3	2	2	3	2	1
	2	2	3	2	2	2	3	3	2	1
	3	2	3	4	3	2	2	2	0	1
	2	2	2	4	3	2	2	2	2	1
	2	2	2	2	3	2	2	2	4	1
22	3	2	3	2	3	2	3	2	2	2
	3	2	2	4	3	2	2	2	2	1
	3	2	3	4	3	2	3	2	0	1
23	3	0	3	4	3	2	3	3	2	1
24	3	2	3	2	4	2	2	4	2	1
25	4	2	3	4	4	2	2	2	2	1
26	3	2	3	4	3	4	3	2	2	1
	3	2	2	4	3	2	3	3	4	1
27	3	2	4	4	4	2	3	3	2	1

[1] For explanation of numerical ratings, see text.

TABLE 6

PATTERN COMPOSITION ON INDIVIDUALS OF *Holacanthus ciliaris*[1]

Total rating	Pattern number									Number of individuals
	1	2	3	4	5	6	7	8	9	
30	4	2	4	4	4	2	4	4	2	1
31	4	2	3	4	4	2	4	4	4	4
32	4	2	2	4	4	4	4	4	4	2
33	4	2	3	4	4	4	4	4	4	8
	4	4	3	4	4	4	4	4	2	3
34	4	2	4	4	4	4	4	4	4	3
	4	4	4	4	4	4	4	4	2	1
	4	4	3	4	3	4	4	4	4	1
35	4	4	3	4	4	4	4	4	4	22
36	4	4	4	4	4	4	4	4	4	13

[1] For explanation of numerical ratings, see text.

great variations, both in the development of a particular pattern, and in the pattern composition of individuals. Of 35, only two individuals possessed the same composition. None possessed a 2 rating for all patterns.

GONADS

Ovaries and testes of specimens of blue angelfishes, intermediates, and queen angelfishes lie upright along the posterior wall of the abdominal cavity and extend forward along the dorsal periphery. They connect with the outside just posterior to the vent. Ovaries are short, thick, and cylindrical; testes are long and ribbon-like. None was noticeably ripe upon gross examination.

Histologically, none of those sectioned was ripe. Most of the ovaries were in a resting stage, with some containing atretic eggs. Most testes were active spermatogenically, with all stages of spermatogenesis, including ripe sperm, present, but were probably not ripe. Testes of two individuals appeared as if spawning had just taken place, due to the complete absence of sperm or developmental stages and the presence of blood cells in some areas.

There seems to be no difference among the ovaries, nor among the testes, of blue angelfishes, intermediates, and queen angelfishes. No excessive amounts of connective tissue, nor aberrant cells, were seen in the gonads of intermediates. Size and shape of the gonads were the same as those of gonads in the blue and the queen angelfishes.

SOCIAL BEHAVIOR

Adult angelfishes are sometimes solitary; more often they form pairs and small groups, or rarely, large aggregations. The fishes in pairs stay within sight of each other, and generally remain in one area. Those

forming small groups congregate around particular obstacles on the bottom, generally coral heads or pilings. Large aggregations are usually made up of gray angelfishes.

Attempts were made several times to collect both individuals of a pair, and in the two times when this was successful (one pair of gray angelfishes and one of French angelfishes), each pair was found to consist of a male and a female. In the gray and French angelfishes, pairs consist always of one species, but in the blue and queen angelfishes, pairs and groups can consist of a mixture of the two species and the intermediate. For instance, on the top of Alligator Reef in the Florida Keys, an adult intermediate was seen pairing with an adult queen angelfish. A color movie made by Dr. Lee Tepley (Lockheed, Palo Alto, California) shows a queen–blue angelfish pair in the Bahamas (probably Turtle Rocks, Bimini).

Under the bridges along the Florida Keys, mixed groups are frequent. Two that were counted consisted of seven blue angelfish and one intermediate, and six blue angelfish and one intermediate. A group composed of blue angelfish, intermediates, and queen angelfish was also seen there.

No references have been found in the literature that suggest the natural spawning behavior of blue or queen angelfishes, and no spawning has been seen during the course of this study. However, if the pairs of fishes seen were spawning pairs, hybridization would occur when the different forms pair. The presence of juveniles of a small size in the habitats throughout the year indicates that spawning occurs year-round.

Habitats

Five habitats were examined during the course of this investigation: inshore channel, bridges, coral heads, reef top, and deep reef. The inshore channel location is an area 3 meters deep in the middle of a side channel lying between Lignumvitae Key and Lower Matecumbe Key, in Florida Bay. The fairly uniform rock bottom, sandy in occasional spots, primarily supports abundant growths of finger sponge, gorgonians, and *Halimeda*, with lesser amounts of other algae and sponges. Currents are swift during ebb and flood tides. Water is usually turbid, and subject to extreme and rapid changes in temperature diurnally and seasonally.

The pilings supporting the bridges between the Florida Keys are characteristically located on a sandy or smooth bare rock bottom; sponges, algae, coral, and other fouling organisms grow on the pilings. Some algae also grow on the bottom. Currents are very swift during tidal flow. The water is fairly clear, or turbid, depending on the state of the tide and the season of the year. Temperature variations are less extreme than farther back in the channels.

Scattered coral heads up to 3 meters across and groups of coral

heads are located in Hawk Channel offshore from Lower Matecumbe Key, in about 3 to 6 meters depth. The solid bedrock, thinly overlain by soft marl in the immediate area of the heads, forms a substrate on which algae, gorgonians and large amounts of *Sargassum* grow. Large numbers of sponges grow on the coral heads, especially on those consolidated into patch reefs. Currents are slight. The water is usually clear, with a moderate seasonal temperature fluctuation.

The shallow (top) portions of the coral reefs located 3 to 5 miles offshore from the Florida Keys are from 1 to 6 meters deep. The bottom is usually composed of very eroded rock densely covered with algae (especially *Dictyota*), with large numbers of gorgonians, and with a large variety of attached and encrusting sponges. Some bare sand channels cut through the rock. Currents are slight. The water is nearly always clear, and temperatures remain relatively uniform throughout the year.

The seaward sides of the reefs, located a short distance from the reef tops, slope steeply from 18 meters down to 33 meters and then stop. Seaward of the abrupt dividing line at about 33 meters depth is a bare, flat, soft marl bottom. The steep slope of the deep reef is typically formed of rock eroded into narrow channels, with fairly dense growths of coral heads and gorgonians, and a small quantity and variety of algae. Currents are very slight, and the water is nearly always clear (usually 20 to 25 meters visibility). Temperature variations are minor, due to the immediate presence of the Florida Current.

Populations

The blue angelfish is generally a continental species, with the bulk of the population found in Bermuda and along the coast of the Americas from North Carolina to Yucatan. The queen angelfish is a more insular form and is abundant in the West Indies and Antilles. Both species occur commonly in the Florida Keys and southeast Florida, but the blue angelfish is much more common. The blue angelfish seems almost completely absent from the Bahamas and Antilles, only three specimens having been caught from Bimini, one from West End, Grand Bahamas Island, and one from Nassau, Bahamas. One other has been recorded from St. Lucia, British West Indies, by Fowler (1915: 546). Intermediates have been collected in Bermuda, South Carolina, eastern Florida, the Florida Keys, Bimini (Bahamas), and St. Eustatius (Dutch West Indies).

Variations occur in relative populations of the blue and queen angelfishes in the habitats available along the Florida Keys. Juvenile blue angelfish are most abundant in the inshore channels and under the bridges, occurring less commonly under coral heads in Hawk Channel. They are rare on the reef top and on the deep reef. Juvenile queen angelfish, on

the other hand, are most abundant on the reef top and the deep reef, less common under the bridges and in the inshore channels, and rare on the coral heads. In the Bahamas, where the inshore water has a more oceanic character, juvenile queen angelfish are very commonly found alongshore.

Adult blue angelfish have a slightly different distribution from juveniles. They are very common in the inshore channels and under the bridges, fairly common on the coral heads and on the deep reef, and uncommon on the reef top. Adult queen angelfish are most abundant on the reef top and the deep reef, fairly common on the coral heads and under the bridges, and rare in the inshore channels. The adult intermediates are found most commonly under the bridges and on the deep reef, are uncommon on the reef top and the coral heads, and are rare in the inshore channels.

Juveniles of the blue and queen angelfishes are solitary and live primarily in and around colonies of finger sponge and *Millepora*. They stay within the confines of the sponge or coral colonies, seldom venturing into open water. Adults are found near and around large obstructions, such as rocks, ledges, pilings, and coral heads, and swim out into open water more freely than juveniles. They seem attracted to any disturbance and quickly congregate around a scuba diver.

Since the angelfishes are not equally abundant in all habitats, counts of juveniles and adults were made in the five above-described habitats, with the emphasis on surveys under the bridges, because the greatest percentages of intermediates seemed to occur here, and because populations here were far higher in density than in any other area. Thirty-one surveys involving 271 adult angelfishes were made in the five habitats (3, 11, 4, 9, and 4 surveys, respectively); the resulting percentages of occurrence are shown below:

	Inshore channel	Bridges	Coral heads	Reef top	Deep reef
Blue angelfish	100%	86.8	93.8	11.9	60.0
Intermediate	0	8.2	0	2.4	6.7
Queen angelfish	0	4.9	6.2	85.7	33.3

The quality of the water varies from continental (inshore channel) to oceanic (deep reef). As indicated by the percentages, the blue angelfish seems to be the only form (as adult) to prefer inshore waters. The reason why this species is also common on the deep reef is not known at the present time. The bulk of the queen angelfish population is located on the reef top and deep reef. Highest proportions of intermediates (and almost all individuals) are located under the bridges and on the deep reef.

Foods

A study of the foods of western Atlantic angelfishes is underway at

the present time. Preliminary results show that the great bulk of the food material ingested is sponges, with a small amount of algae, and traces of hydroids and gorgonians. The species of sponges and algae eaten vary with the habitat, but their presence in stomach contents indicates that both species of angelfishes are primarily feeding on the same range of food organisms.

A number of times, individuals of all three forms have been observed biting the same sponge together and in succession.

In the Florida Keys, sponges are very abundant in the habitats studied. In areas where sponges are few, so too are the angelfishes. Every specimen of angelfish examined, that was caught during the day, contained large amounts of food.

Conclusions

The blue and queen angelfishes, due to their essential retention of species characters in this area of sympatry, are judged to be valid species. The individuals, designated as intermediates in this paper, that show color patterns intermediate between those of adult blue and queen angelfishes, are hybrids derived from these two species. The broad, low form of the frequency curve for the hybrids is as expected, considering the variation within each species. The presence of gaps between the hybrids and the parental species in the distribution of total ratings (Fig. 11) suggests that there is no effective backcrossing and that there is no reason to suspect introgression as accounting for some variation in the parental species.

The available evidence from gonadal material indicates that these hybrids are potentially viable, and the observations on behavior indicate that cross-spawning is likely to occur.

Ecology of the two species seems to overlap so greatly that hybrids could easily survive in proximity to the parent species, especially since observations in the field indicate that aggressive behavior among adults is minimal.

Both the blue angelfish (a continental species) and the queen angelfish (an insular species) had more restricted ranges during the Recent Wisconsin glaciation. In reinvading northern areas following the retreat of the ice sheet, they have come in contact in southern Florida and other areas, and hybridization has resulted. However, the two species have maintained their identities; no effective introgression has occurred. The factors leading to the initial separation and speciation of the blue and the queen angelfishes are unclear but the difference in ecology likely is a secondary facet brought about by contact between the two closely related species.

Discussion

Similar distribution patterns are seen in the other species of western Atlantic angelfishes, but hybrids between them are unknown. The gray

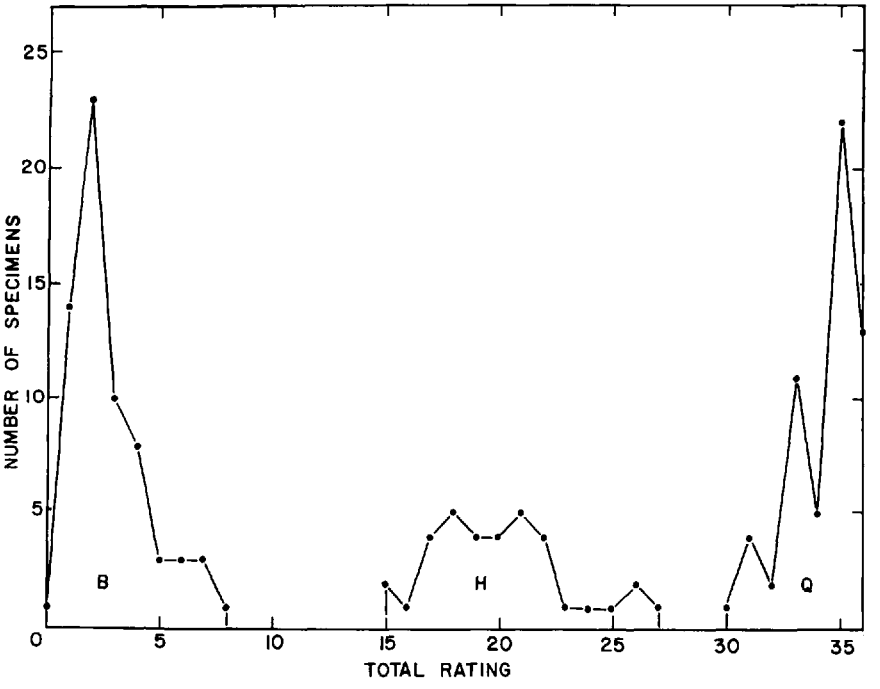

FIGURE 11. Frequency distribution of totaled ratings for adults of the blue angelfish (B), the queen angelfish (Q), and the hybrid form (H).

and the French angelfishes are common in Florida and the Antilles, and commonly occur together with no apparent differential habitat preference. The species seem as closely related to each other as the blue angelfish is to the queen angelfish, yet no hybrids have been found, and all specimens can be reliably identified. Both species have been introduced into Bermuda, according to Beebe & Tee-Van (1933: 261-262), yet no intermediates have been recorded.

The rock beauty is common alongshore and on the reefs in the Bahamas and the Antilles, but in Florida it only inhabits the offshore reefs. It has never been seen by the author inshore around the Florida Keys, or even in Hawk Channel.

The pigmy angelfish is common in shallow and deep waters of the Bahamas and the Antilles, but has only recently been found living on the deep reefs of southern Florida in 70- to 100-feet depths. A single specimen has been found, however, on the top of Alligator Reef. Apparently this species is even more intolerant of inshore conditions than the rock beauty and may only now be in the first stages of reinvading Florida waters from the Bahamas.

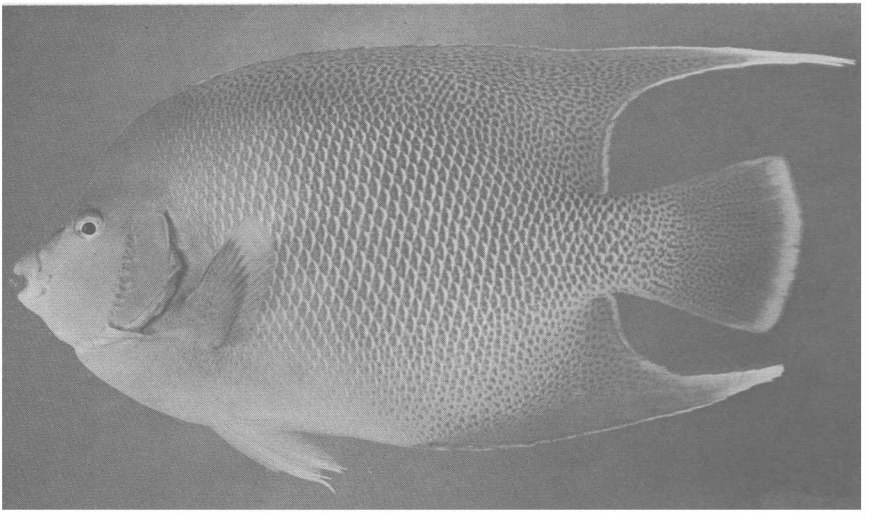

FIGURE 12. An adult of the blue angelfish, *Holacanthus isabelita,* 208 mm SL, total rating of 1 on a numerical scale of 0 to 36.

Nichols & Mowbray (1914) described an adult angelfish of intermediate coloration under the name *Angelichthys townsendi.* Their color description is as follows:

> Color when fresh grayish-green, lips, interorbital, upper margin of opercle, spines of head, breast, and base of pectorals light blue, cheeks and opercle pale greenish blue, inner and outer margins of vertical fins edged with bright blue, an orange stripe beginning at the base of first dorsal spine extending to produced rays, a similar less conspicuous stripe on anal, pectoral and caudal lemon yellow, ventrals very pale yellow, angle of mouth and membrane at angle of opercle orange, eye golden, extreme base of pectoral sky blue, region immediately behind pectoral bright yellow, the margins of the larger scales edged with yellow, forming diagonal lines across the body. Membrane on lower limb of opercle orange.

Goode (1876: 43-44) gave the following color description of his new form *H. ciliaris,* var. *Bermudensis*:

> Brown with a shade of olive-green, each scale edged with a lighter tint; on the dorsal and anal fins, the brown has reddish tinge. Chin, nape, base of pectoral, borders, and spines of operculum and preoperculum, bright cobalt blue. Extremity of pectorals, bright yellow. Borders of dorsal and anal bright blue, passing through a vivid green to bright yellow on the slender streamers formed by the prolongations of the soft dorsal and anal fins. Caudal bright yellow, with narrow border of greenish blue. Base of ventrals blue, passing through green into yellow at the extremities. Young and half-grown individuals are ornamented with three

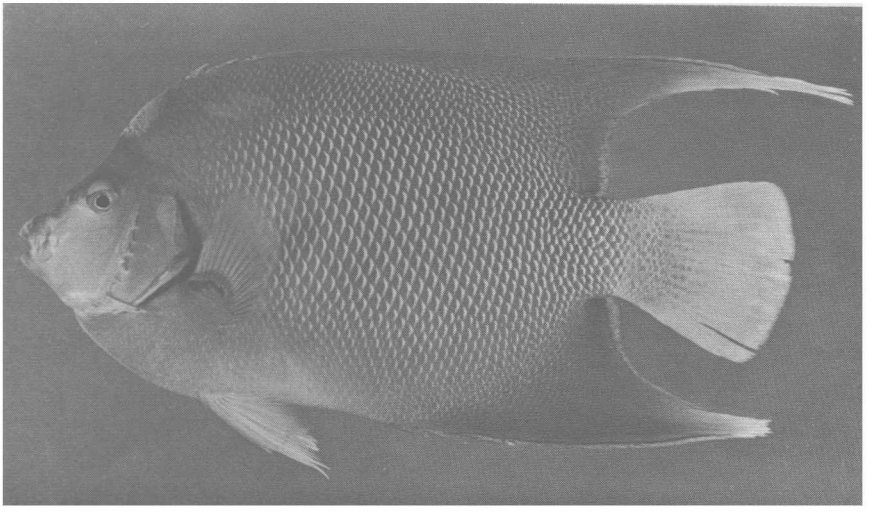

FIGURE 13. An adult of the hybrid, *Holacanthus isabelita* × *H. ciliaris,* 187 mm SL, total rating of 18 on a numerical scale of 0 to 36.

or four broad transverse bands of blue and yellow. My specimens, some 12 in number, differ from all descriptions in the absence of the spot of brown, encircled with blue, on the nape.

Goode's description is presumably of a fish that has acquired the adult's coloration. However, an examination of the type specimens (three cotypes, USNM 154852) shows that only one (126 mm SL) has an adult's color characters. This specimen has intermediate coloration on the opercle and on the anal fin. The two other specimens (107 and 90.6 mm SL) still possess coloration transitional between juvenile and adult, but also possess hybrid tendencies in the coloration of the operculum, and possibly of the pectoral and anal fins. Unfortunately, all three specimens are extensively decolorized. The colors in the original description indicate that the specimens were preserved and partially decolorized when they were described.

Due to the probable hybrid nature of these type specimens and to the confusing color description by Goode, it is necessary to replace the name *Holacanthus bermudensis* Goode, 1876, with *Holacanthus isabelita* (Jordan & Rutter) (*in* Jordan & Evermann, 1896: 420, and 1898: 1684-1686). This latter description, although brief, unmistakably refers to an adult blue angelfish. The description of *Holacanthus townsendi,* and an examination of the holotype (AMNH 4751), leads to the conclusion that this species name is based on a hybrid.

Randall (1956) investigated what appears to be a parallel situation

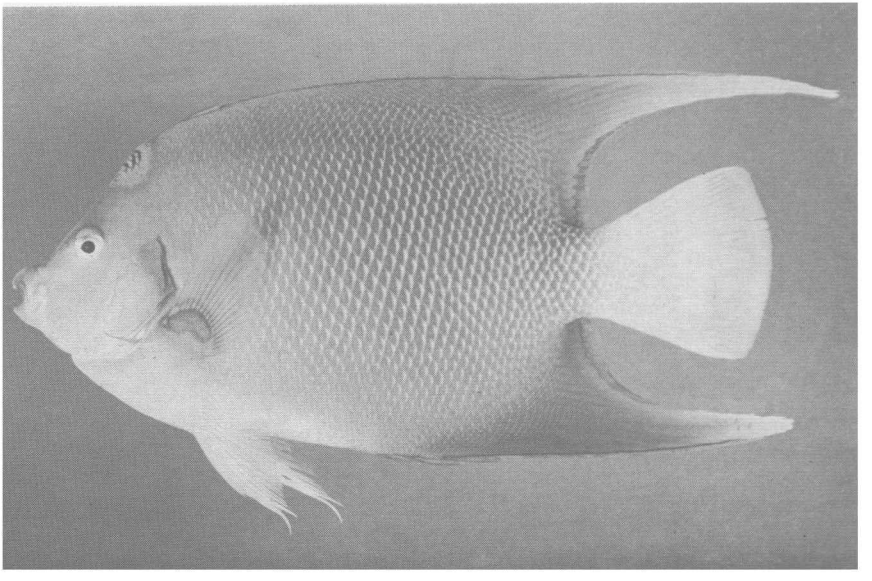

FIGURE 14. An adult of the hybrid, *Holacanthus isabelita* × *H. ciliaris*, 175 mm SL, total rating of 26 on a numerical scale of 0 to 36.

of hybridization in the Phoenix Islands, as far as ecology of the populations and the appearance of the intermediate individuals is concerned. Here, two species of surgeonfishes live sympatrically, but one is characteristic of surge channels in the reef, with the other most abundant on the inshore part of the coralliferous terrace. Both species eat essentially the same foods and spawn throughout the year. Three intermediate specimens were collected, with intermediacy shown in morphology (shape of caudal fin) and in coloration (seven patterns).

Raney (1957) obtained and analyzed the total population of pickerels in a Massachusetts pond and found that two species were present, as well as a large number of hybrids and backcrosses to each parent. Many otherwise typical specimens of the larger species, *Esox niger,* had irregularities in the color pattern, attributed to introgressed genes. Relative populations were: 123 specimens of *E. niger,* 18 specimens backcrossed to *E. niger,* 22 specimens of the intermediate hybrid, 13 specimens backcrossed to *E. americanus* and 8 specimens of *E. americanus.*

According to Hubbs (1955), natural interspecific hybrids are intermediate between their parental species in all characters in which those species differ, except for some features that reflect hybrid vigor. Intermediacy is seen in the coloration, the general body form, the size of the head, the length and protrusion of the snout, the size of the scales,

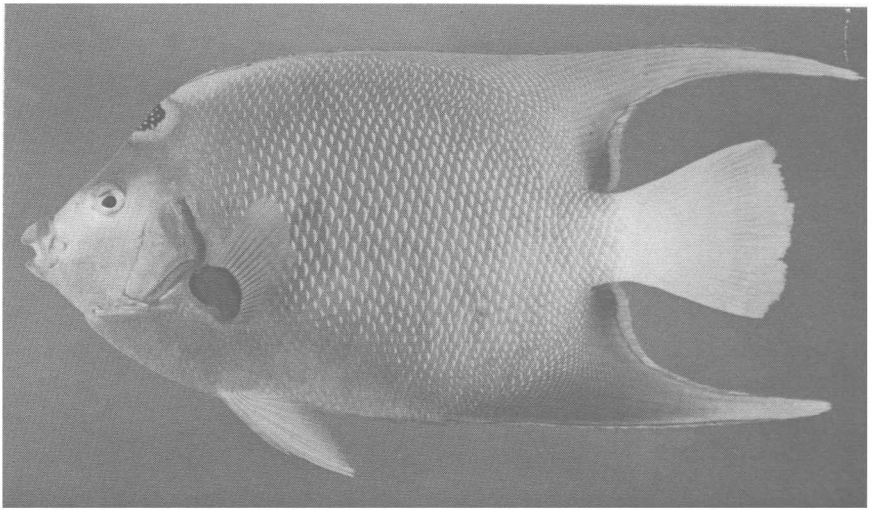

FIGURE 15. An adult of the queen angelfish, *Holacanthus ciliaris*, 201 mm SL, total rating of 36 on a numerical scale of 0 to 36.

structure of the lips, type of relative growth, and internal characters such as the skeleton. Hybridization is often a function of the intergradation of the habitat—species segregated in breeding by differential responses to any physical, chemical, or organic features of the environment tend to breed together where the environment is rendered intermediate, either through natural causes or through modifications by man. Anderson (1949: 13-14) said that habitat preferences are inherited in substantially the same manner as any other character, and in any cross between species, the differences that allow them to fit into different habitats segregate in the same manner as morphological ones.

Bridge pilings in the Florida Keys are artificial objects which would not normally have occurred in the channels. The prevalence of hybrids around them may reflect a "hybridization" of the environment. The pilings afford excellent protection to adult angelfishes and with their lush growths of sponges and other organisms afford a rich source of food. Here, the common presence of the three forms of angelfishes seems to have enhanced the interspecific grouping of individuals.

Additional studies still need to be made on the natural spawning behavior of these fishes and on the resulting young.

SUMMARY

No external meristic character has been found that will distinguish between all individuals of the two species of angelfishes, *Holacanthus*

isabelita and *H. ciliaris*, but counts of dorsal- and anal-fin rays will aid in identifying most of them. There is some differentiation between large individuals of the two species in certain aspects of morphology, such as the sizes of the preopercular spines and the outline of the nape.

The only reliable method of distinguishing these species is by the coloration. Juveniles can be separated by the degree of curvature of the fourth major bluish-white bar. Adults of one species differ drastically in coloration from juveniles, and from adults of the other species.

Adults with coloration intermediate between that of *H. isabelita* and *H. ciliaris* are present in the environment. An analysis of these intermediates was made, using coloration of: the nape, the area around the bases of anterior dorsal-fin spines, the iris of the eye, the edge of the operculum, the base and rays of the pectoral fin, the exposed portion of the large scales of the body, the last few rays of the anal fin, and the caudal fin. One morphological character—sizes of preopercular spines—was also used. The variations of each pattern were assigned numbers from zero to four, depending on the degree of development. Analyses of pattern compositions indicate that individuals of both *H. isabelita* and *H. ciliaris* possess some conservative patterns, and others that are somewhat variable. Most patterns occurring on the intermediates are very variable.

Individuals of *H. isabelita* and *H. ciliaris* form pairs which are probably each composed of a male and a female. They also form small groups. Many of these pairs and groups are composed of more than one of these species, and may also include intermediates.

Counts of individuals of the two species and the intermediate in five habitats in the Florida Keys reveal that relative populations of each form vary in each habitat, but that those of *H. isabelita* are by far the largest, except on the reef top.

H. isabelita and *H. ciliaris* are valid species. The intermediates are hybrids resulting from spawnings between these two species. There appears to be little effective backcrossing to either parental species.

The type and original description of *Holacanthus townsendi* (Nichols & Mowbray, 1914) refer to a hybrid between *H. isabelita* and *H. ciliaris*.

The types and original description of *Holacanthus ciliaris*, var. *Bermudensis* most likely refer to hybrids. Therefore this name has been replaced by *Holacanthus isabelita* (Jordan & Rutter, 1896) to designate the blue angelfish.

SUMARIO

HIBRIDACION ENTRE LOS PECES *Holacanthus isabelita* Y *H. ciliaris* DEL ATLANTICO OCCIDENTAL

No se ha encontrado carácter merístico externo que sirva de distinción

entre todos los individuos de las dos especies *Holacanthus isabelita* y *H. ciliaris* pero el conteo de los radios de las aletas dorsal y anal podrá ayudar a la identificación de la mayoría de ellos.

Entre los individuos grandes de las dos especies hay alguna diferenciación en ciertos aspectos de la morfología, tal como el tamaño de las espinas preoperculares y el contorno de la nuca.

El único método seguro para distinguir estas especies es por la coloración. Los jóvenes pueden distinguirse por el grado de curvatura de la cuarta barra mayor blanco azulosa. Los adultos difieren drásticamente en coloración de los jóvenes de su especie y de los adultos de la otra especie.

Adultos con coloración intermedia entre la de *H. isabelita* y *H. ciliaris* están presentes en el mismo ambiente. Se hizo un análisis de estas formas intermedias usando la coloración de: la nuca, el área alrededor de la base de las espinas de la aleta dorsal anterior, el iris del ojo, el borde del opérculo, la base y radios de la aleta pectoral, la parte expuesta de las escamas grandes del cuerpo, los últimos radios de la aleta anal y la aleta caudal. También se usó un carácter morfológico, el tamaño de las espinas preoperculares.

A las variaciones de cada patrón se le asignaron números, del cero al cuatro, dependiendo del grado de desarrollo. El análisis de las composiciones de cada patrón indica que los individuos de ambas especies, *H. isabelita* y *H. ciliaris,* poseen algunos patrones conservadores y otros que son algo variables. La mayoría de los patrones que se presentan en los intermedios son muy variables.

Los individuos de *H. isabelita* y *H. ciliaris* forman parejas que están probablemente compuestas de un macho y una hembra. También forman pequeños grupos. Muchas de estas parejas y grupos están constituídas por más de una especie y también pueden incluir intermedios.

El conteo de individuos de las dos especies y de la forma intermedia en cinco habitats en los Cayos de la Florida, revela que la población relativa de cada forma varía en cada habitat, pero que las de *H. isabelita* son con mucho las mayores, excepto en la parte superior del arrecife.

H. isabelita y *H. ciliaris* son especies válidas. Los intermedios son híbridos resultantes del cruce de estas dos especies. Parece ser que hay poco cruzamiento retrógrado efectivo a cualquiera de las especies progenitoras.

El tipo y la descripción original de *Holacanthus townsendi* (Nichols & Mowbray, 1914) se refiere a un híbrido de *H. isabelita* y *H. ciliaris.*

Los tipos y la descripción original de *Holacanthus ciliaris,* var. *Bermudensis,* probablemente se refiere a híbridos. Por tanto este nombre ha sido reemplazado por *Holacanthus isabelita* (Jordan & Rutter, 1896) para designar a la especie de color azul.

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